

RECONSTRUCTION OF A SPECIFIC EXAMPLE OF INSECT
INVASION WAVES: THE CLADISTIC ANALYSIS OF *CANTHON*
(COLEOPTERA: SCARABAEIDAE) AND RELATED GENERA
IN NORTH AMERICA¹

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ABSTRACT

The historical biogeography of insects of the Mexican Transition Zone is extremely complex. Holarctic, Nearctic and Neotropical lines seem to have invaded and speciated in the area at different times. The neotropical lines in particular are thought to have invaded the Mexican Transition Zone from South America on two occasions, one during the Miocene, the other during Plio-Pleistocene. The subgenus *Canthon* and its closely related taxa, the subgenus *Boreocanthon* and the genus *Melanocanthon*, as well as the subgenus *Glaphyrocantion*, have been proposed as an example for the analysis of this process.

The implications from such an event allow predictions regarding the phylogenesis and ecological evolution of these three taxa, as follows. First, the proposed Miocene invasion lineage(s) shared a common history and diversified in the biomes that evolved in North America during the Miocene and Pliocene. Second, those species which diversified from a common ancestor form a phylogenetically related group that reflects the history of the group in accordance with the history of the area and biomes which they occupy. Third, the species stemming from the proposed South American Plio-Pleistocene invasion evolved under a different set of ecological and biogeographic conditions, and as such are distantly related in phylogenetic terms to the members of the first invasions wave. Fourth, consequently, in a cladogram including species of both invasion waves, the Plio-Pleistocene elements branch at the base of the tree. Fifth, moreover, the branching sequence of the cladogram is not in concordance with the estimated age of appearance of the different biomes which the species occupy. These five predictions were supported in the present study, by the species cladogram. The

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results of this analysis therefore lend support to the hypothesis of two waves of invasions of the Mexican Transition Zone by Neotropical elements from South America.

RESUMEN

La zona de Transición Mexicana es un área de gran complejidad ecológica, geológica y biogeográfica. En relación a su dinámica zoogeográfica, Halffter (1962, 1964, 1972, 1974, 1976, 1978 y 1987) ha propuesto una serie de hipótesis basadas en las relaciones taxonómicas, riqueza específica, historia geológica y patrones de distribución de diferentes grupos de insectos, en las que señala que diferentes linajes de origen holártico, neártico y neotropical invadieron esta zona en diferentes épocas. En el caso específico de los linajes neotropicales, considera dos invasiones mayores, una durante el Mioceno, la segunda del Plio-Pleistoceno al actual. El subgénero *Canthon* y otros dos taxa muy emparentados, el subgénero *Boreocanthon* y el género *Melanocanthon*, al igual que el subgénero *Glaphyrocantion*, son buena evidencia de estas dos invasiones. Los invasores miocénicos se encuentran en biomas que comenzaron a originarse en este período, como es el caso de formaciones áridas, pastizales, bosques de encino-piñón y bosques templados decídúos; o en épocas más recientes, pliocénicas, como bosques de pino y pino-encino (Axelrod, 1975, 1979). Las líneas propuestas como invasoras plio-pleistocénicas o posteriores se encuentran distribuidas principalmente en biomas de penetración reciente, como las selvas tropicales, sobre todo la selva alta perennifolia (Germeraad *et al.*, 1968; Graham, 1973, 1981; Toledo, 1976, 1982; Gentry, 1982; Prance, 1982). En base a estudios biogeográficos y taxonómicos anteriores (Halffter, 1958, 1961, 1962, 1972, 1974, 1976; Halffter y Martínez, 1966, 1967, 1968, 1977) se propone que las siguientes especies del subgénero *Canthon*: *humectus*, *pilularius*, *imitator*, *vigilans*, *chalcites* y *obliquus* así como el subgénero *Boreocanthon* y el género *Melanocanthon* han derivado de la invasión miocénica. Las especies *indigaceus*, *cyanelus* y *morsei* del subgénero *Canthon* y el subgénero *Glaphyrocantion* se consideran parte de la invasión plio-pleistocénica.

El objetivo de este estudio es aportar una nueva evidencia que apoye la existencia de los dos procesos invasores por elementos neotropicales a la Zona de Transición Mexicana, a partir de un análisis cladístico del subgénero *Canthon* y taxa cercanos. El análisis cladístico puede apoyar o no las predicciones que emanen de las hipótesis biogeográficas.

Con respecto a las invasiones neotropicales pueden establecerse dos hipótesis complementarias. La primera consideraría la posibilidad de que a partir de la línea miocénica ocurriera una diversificación congruente con la aparición de zonas adaptativas disponibles (Simpson, 1953), creadas por el surgimiento de nuevos biomas. La diversificación de especies originada a partir de un ancestro común resultaría en un grupo filogenéticamente emparentado (Hennig, 1966; Wiley, 1981), cuyo cladograma reflejaría la historia evolutiva del mismo y presentaría un mayor o menor grado de concordancia con la historia del área y de los biomas que ocupan las especies. La segunda hipótesis supondría que los invasores plio-pleistocénicos, al tener una historia ecológica y evolutiva diferente a la de los miocénicos, presentaría relaciones filogenéticas distintas y una distribución geográfica y ecológica también diferente. Por ello, al construirse el cladograma, los invasores plio-pleistocénicos se encontrarán en la base la ramificación del árbol y no existirá congruencia directa entre la secuencia de ramificación del cladograma y la secuencia de aparición de los diferentes biomas en Norteamérica.

El análisis cladístico (Fig. 2) se basa en 29 especies y 29 caracteres (Cuadro I) y emplea el paquete de análisis filogenético PAUP. Los caracteres no fueron codificados en forma ordenada,

ya que estamos de acuerdo con Meacham (1984) en que la polarización de caracteres no se puede definir con certitud. La base del cladograma fue determinada utilizando el subgénero *Glaphyrocanthon* como grupo externo. La decisión de elegir a este subgénero como grupo externo se encuentra fundamentada por los resultados de la estimación del grado de similitud de todos los géneros y subgéneros de los componentes americanos de la tribu *Canthonina* indicado en la Fig. 1. Cincuenta cladogramas igualmente parsimoniosos fueron obtenidos. Posteriormente se utilizó el programa CONTREE para establecer un cladograma de consenso "estricto" (Rohlf, 1982) (Fig. 2). También se obtuvo un cladograma siguiendo el método de consenso de Adams (1972), pero no fué incluido en este estudio por ser muy semejante al primero.

El cladograma de consenso obtenido fue correlacionado con los diferentes biomas (Fig. 2) en donde se encuentran distribuidas las especies (Mapas 1-7) y su análisis concuerda con las predicciones de la existencia de dos líneas invasoras neotropicales en Norteamérica.

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INTRODUCTION

The dynamics of insect biogeography in the Mexican Transition Zone (hereafter referred to as MTZ; Halffter, 1976), which includes the southwestern United States, all of México and a large part of Central America extending to the Nicaraguan lowlands, are of great complexity. The MTZ is species-rich because of the great variety of environments and ecological refuges available and presents a complex and varied overlap of the Neotropical and Nearctic faunas. The area is also an important part of the north-south dispersal corridor for faunas and floras of diverse origin that have dispersed during different geological eras between North and South America (Stehli and Webb, 1985).

Halffter (1962, 1964, 1972, 1974, 1976, 1978, 1987) has developed a set of hypotheses to explain comprehensively the distribution of insects in the MTZ. His inferences, based on taxonomic relationships, species richness, geological history and distribution patterns derived for several insect groups, support the notion that the present insect fauna of the MTZ has originated from multiple invasions and *in situ* speciation at different times from Nearctic, Holarctic and Neotropical lines, conferring on this region a mixed transitional character in insect

composition. The Neotropical lines which invaded North America from South America are thought to be represented by a Miocene and by a Plio-Pleistocene component (Halffter, 1972, 1974, 1976). These components show distinctive geographic patterns, the distribution cores of which are centered on areas defined by actual ecological conditions.

Geological support for the possibility of migration between the American land-masses has been summarized recently. Donnelly (1988) presents a scenario constructed from the concordant features of the diverse and conflicting analyses made for the Caribbean and Central American Bridge and concludes that faunal movements requiring short (tens of kilometers) overwater dispersal conditions might have occurred during brief intervals during the late Cretaceous through a proto-Antillean arc and during the middle Cenozoic through Central America. Overland dispersal became possible when the Central American Land Bridge was finally consolidated at the beginning of the Pliocene, about 5.7 m.y. B.P. (Kaneps, 1979), or late Pliocene, 3 m.y. B.P. (Webb, 1977, 1978; Keigwin, 1978; Marshall *et al.*, 1982). Biological evidence presented by Savage (1982) suggests a connection between North and South America early in the Cenozoic, based on inferred concordant dispersal to Central America of South American organisms such as angiosperms, fishes, amphibians and reptiles. Mammals, however, did not exhibit the same patterns. Nevertheless, some evidence indicates that mammals had a limited dispersal between North and South America in the late Cretaceous and again in the Oligocene, that increased during the late Miocene, and culminated in an extensive faunal interchange in the Pliocene (Stehli and Webb, 1985).

One of the examples given by Halffter (*op. cit.*) of a Neotropical invasion into North America in two waves, one during Miocene, the other during Plio-Pleistocene, is the genus *Canthon*. This taxon belongs to the subtribe Canthonina, which, together with three other subtribes, is grouped into the tribe Scarabaeini. It is characteristic of adults of the tribe Scarabaeini to have fine, long and bowed metatibiae, used by most species to roll food balls made from droppings (mostly mammalian) or small carcasses, the latter being more common in the Neotropical Region. Members of this group do not show marked sexual dimorphism, a fact that contrasts strikingly with the situation characteristic of other tribes. Most of these species form balls at the food source. Subsequently, this ball is rolled and buried at a shallow depth. This same process is followed by many of the species for nesting; ball-rolling is then carried out by a bisexual pair.

The subtribe Canthonina has a Gondwanian distribution. More than half of all the species of Canthonina are Neotropical, as well as 27 of 28 American genera (Halffter and Edmonds, 1982). The subtribe is also richly represented in Australia, South Africa and Madagascar. The other Ethiopian and Oriental faunas are less rich, a consequence of strong competition or perhaps ecological replacement from other tribes of ball-rolling beetles.

ASSUMPTIONS

The biogeographic analyses of the MTZ by Halffter (*op. cit.*) and the taxonomic study of the American *Canthon* by Halffter (1958, 1961) and Halffter and Martínez (1966, 1967, 1968, 1977), suggests that some North American species of the subgenus *Canthon* (*C. humectus*, *obliquus*, *chalcites*, *imitator*, *pilularius*, and *vigilans*), all species of the closely related subgenus *Boreocanthon*, and those of the genus *Melanocanthon* originate from an ancestral Miocene invasion from South America, and that the species *C. indigaceus*, *C. cyanellus* and *C. morsei*, of subgenus *Canthon*, as well as the subgenus *Glaphyrocانthon*, represent recent Plio-Pleistocene invaders into North America. We accept these suggestions.

PREDICTIONS

The MTZ biogeographic scenario as proposed by Halffter (*op. cit.*) allows predictions for *Canthon*, *Boreocanthon* and *Melanocanthon*, concerning phylogenesis and ecological evolution in North America. These predictions can be tested by Methods outlined below.

Prediction 1.

Beginning with the proposed migration wave from South into North America by an ancestral *Canthon* component in Miocene time along a discontinuous corridor formed by islands (Briggs, 1987; Donnelly, 1988), this area would have varied in its ability to allow the passage of some elements into North America, and thus would have isolated these elements from their ancestral lineages in South America. Therefore, this Miocene component would have been subjected to the same macroecological pressures for a prolonged period of time, would have lived under the same physiographic conditions and would have had a common biogeographic history in North America.

Prediction 2.

Several biomes originated in North America during Miocene times, such as arid zones, grasslands, piñon-oak woodland and hardwood forest (Axelrod, 1975, 1979). Other biomes started evolving in North America in the Pliocene, such as pine and pine-oak forests (Axelrod, 1975, 1979). These emerging biomes would represent newly-available habitats and one could expect species diversification to occur in the invading line(s) (Simpson, 1953). If this species diversification originated from one common Miocene ancestor, one can consider also on the basis of phylogenetic tenets (Hennig, 1966; Wiley, 1981) that the derived species form groupings which are phylogenetically related to each other and reflect the historical course of speciation.

Prediction 3.

Those species that are thought to be derived from this Miocene invasion and that have diversified in the new adaptive zones, exhibit relationships that reflect some degree of congruence with the historical sequence of biome appearance in which the species now live, as has been postulated for area cladograms (Rosen, 1978, 1979).

Prediction 4.

Species *C. cyanellus*, *C. indigaceus* and *C. morsei*, of subgenus *Canthon*, are considered to be derived from a Plio-Pleistocene invasion from South America (Halffter, 1961, 1962, 1964, 1972, 1974, 1976; Halffter and Martínez, 1977) associated with several types of tropical forest, and in particular with rainforest. The association with the tropical forest suggests that those three *Canthon* species are South American taxa which have enjoyed range expansions during and after the closing of the Isthmus of Panamá (Liebherr, 1988). These tropical species should be distantly related in phylogenetic terms to the members of the Miocene invasion waves, because they evolved under a different set of ecological and biogeographic conditions. This permits that these species branch at the base of the species-tree and cause the cladogram branching sequence to be in disorder in relation to the age of appearance of the different biomes in which the species now live and therefore be incongruent with the biogeographic history of the area, since they may represent different phyletic lines. This prediction and those put forward for the Miocene lineage of invasion can be compared with the results of the concordance between the cladogram and the biome evolution sequence as a test of the MTZ insect biogeographical hypothesis.

MATERIAL AND METHODS

Material

This study is the result of the examination of several thousands of specimens of American *Canthonina*. All North American species of the subgenera *Canthon* and *Boreocanthon*, the majority of *Glaphyrocantthon*, as well as the totality of the *Melanocanthon*, were studied for the cladistic analysis. Many representative species of American genera and subgenera of *Canthonina* were studied for the phenetic analysis.

All this material comes from the G. Halffter collection, Xalapa, México, which is one of the best collections for this group.

Terminal Taxa.— We accept the diagnoses given by Halffter and Martínez (1977) for the genus *Canthon* and the subgenera *Canthon*, *Boreocanthon* and *Glaphyrocantthon* as well as the genus *Melanocanthon*. With the exception of some mentioned later on, the species included in these genera and subgenera in North America are those assigned in the earlier papers of Halffter and Martínez (1977) and Halffter (1958, 1961).

Terminal taxa so defined are listed in Table II. Halffter and Martínez (1977) consider *Canthon (Boreocanthon) bisignatus* Balthasar as a doubtful member of the

subgenus *Boreocanthon*. This species is not included in the analysis as only a scanty description of it is available and we have been unable to obtain additional material. A second species of subgenus *Boreocanthon* that has been excluded is *B. nyctelius* Bates, since Howden (1966) considers it to be conspecific with *C. puncticollis* Le Conte. Lastly *C. forreri* Bates is almost identical to *C. integricollis* Schaeffer, and for this reason it is not included in our analysis.

We consider *Glaphyrocanthon* as a convenient external group to root the cladogram. This subgenus is composed mainly of species of South American origin with a limited penetration into North America. A phenetic analysis (Fig. 1 and Appendix) shows that *Glaphyrocanthon* has rather distant relationships with the other genera and subgenera considered in this analysis and can be considered safely as an outgroup.

Cladistic Methods.

The cladistic analysis based on the data presented in Tables I and II was carried out using the PAUP (Phylogenetic Analysis Using Parsimony) computer program, version 2.4.0 (1985), distributed by Dr. L. Swofford (Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820), and run on a VAX 8700 computer employing the following options: NOTU=29; NCHAR=29; ROOT=OUTGROUP; GO/SWAP=GLOBAL; MULPARS; CONFILE; MAXTREE=50; ALL CHARACTERS UNORDERED. Subsequently Swofford's CONTREE program (Version 1/3/86, distributed with PAUP) was used to calculate Adams and strict consensus trees from the multiple trees that resulted from the PAUP analysis.

Characters.— Of the twenty-nine characters employed, twenty-three were binary and six multistate. Unordered multistate characters represent no problem for a cladistic analysis using PAUP. The majority of characters are derived from Halffter (1958, 1961) but, some of them derive from personal (B.K.) observations.

For the present analysis all characters were coded as unordered, since sister groups in and outside *Canthonina* are not yet defined, thus rendering the character transformation series unknown. Character polarities can be determined subsequently by rooting the tree with an outgroup using the parsimony criterion (Swofford, 1985). However, Meacham (1984) has argued that character polarities are not known with certainty. We consider that an analysis of character polarity under such circumstances would not be very informative, since we are analyzing only a few species and the results could be misleading. For this reason we have not attempted to determine character polarities.

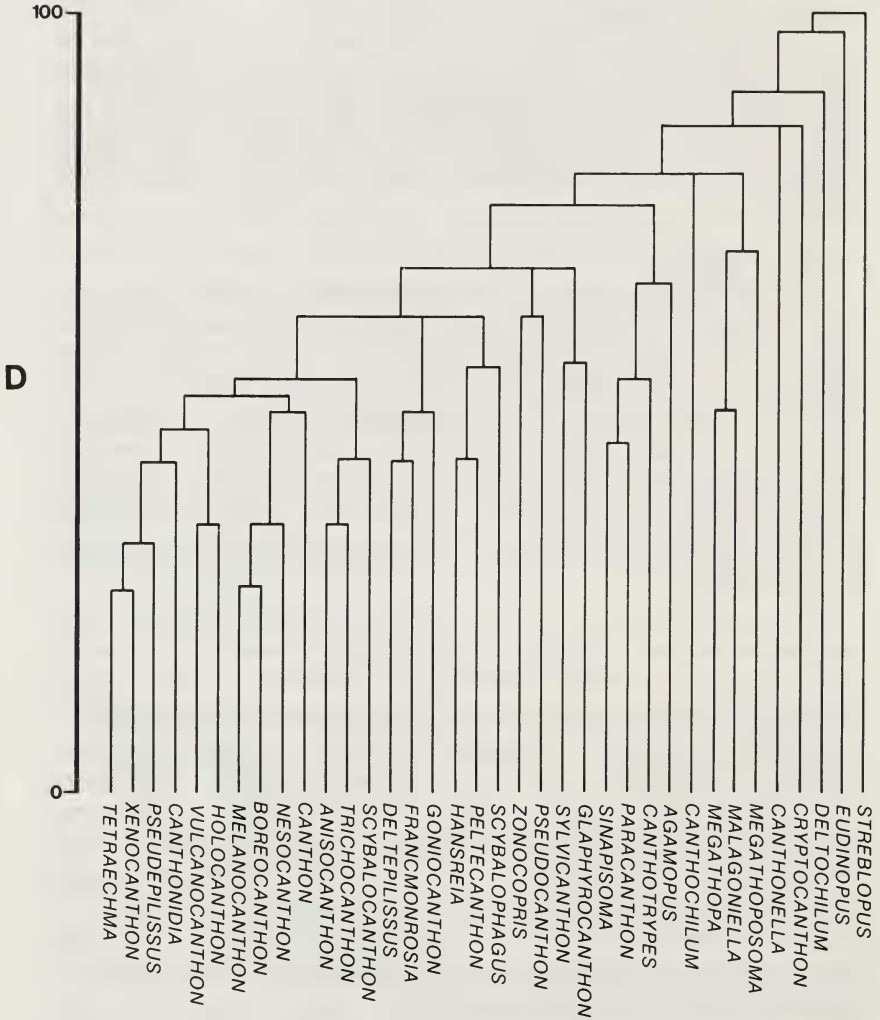


Fig. 1. Phenogram of the genera and subgenera of the American Canthonina. The scale measures the dissimilarity (D) between taxa based on the Manhattan metric. The phenogram has been constructed according to the UPGMA clustering procedure.

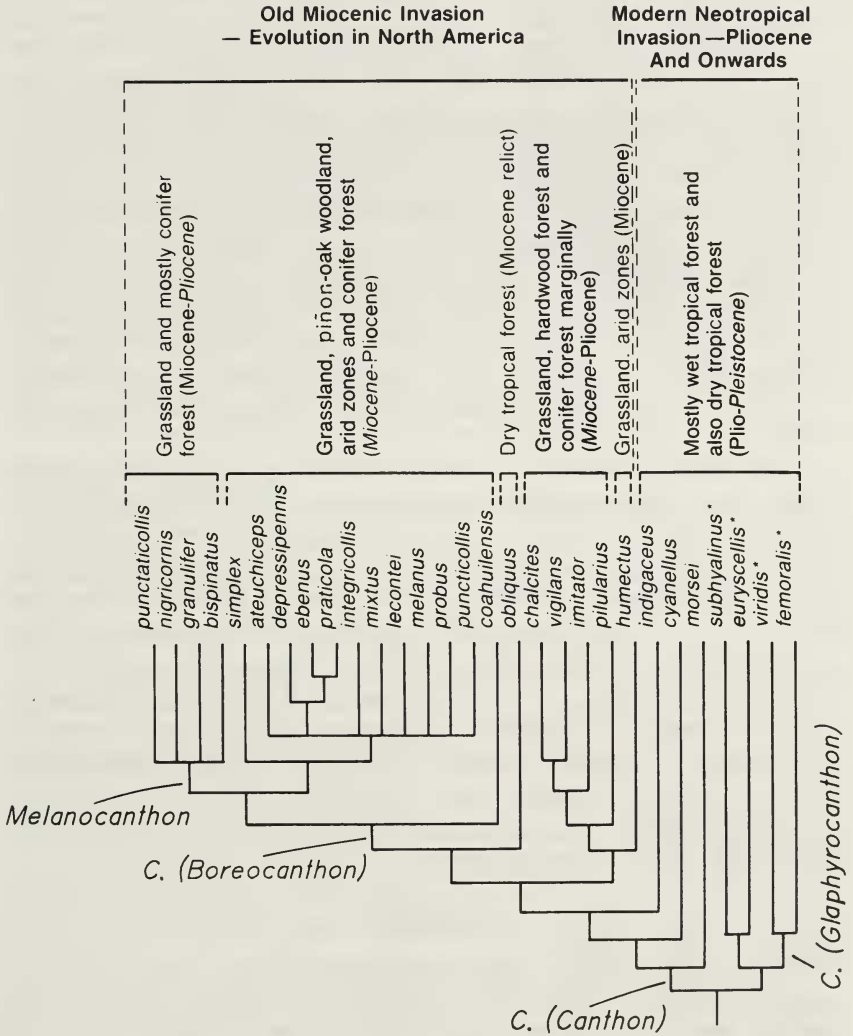


Fig. 2. Strict consensus cladogram of the North American species of the subgenus *Canthon* and related taxa of the subgenus *Boreocanthon* and the genus *Melanocanthon*. The distribution of the taxa in different biomes is indicated as well as the inferred age of appearance of the biome in North America. The age of appearance of biomes correlated with the greatest number of associated species is in italics. The proposed invasion time of the different lines into North America are also indicated. Species marked with a star represent outgroups used for rooting the cladogram. The length of the cladogram branches have no meaning.

Zoogeographic Methods.

The subject of this paper is to examine further evidence regarding the interpretation of two different dispersal waves in the speciation process of the subgenus *Canthon* and its closely related taxa *Boreocanthon* and *Melanocanthon* in relation to the biogeographical history of the MTZ as put forward by Halffter. Broadly, the biogeographic history of the dung-rollers under study in North America is inferred from a cladistic analysis and related to the sequence of the age of appearance of the different biomes where they are distributed now. More particularly, the cladogram of all species pertaining to a taxon (including or not other related taxa) which is distributed in defined study areas is constructed. Then we relate the cladogram with the sequence of events suggested by the age of appearance of the different biomes where the dung-rollers live now and compare it with the predictions stemming from the MTZ hypotheses, in order to gain some insight into vicariant and dispersal events that have taken place in the area.

Two other approaches for reconstructing the biogeographic and ecological history of taxa using a phylogenetic-tree analysis have been proposed (Brooks, 1985, Legendre, 1986). Brooks' method treats species as characters of the areas in which they occur and lineages of species are thus considered transformation series linking different areas in an historical pattern. Legendre (1986) reconstructs the dispersal of a community into adjacent territories by using data of species presence/absence, obtaining tree-like structures of dispersal from a single trunk. Connor (1988) analyzes and gives a summary of the bases for inferring the historical dynamics of biogeographic distributions using phylogenetic methods. For vicariance biogeography (Nelson, 1973, 1975, 1978) incongruent patterns between the area cladograms of two or more groups may be interpreted as dispersal, but different modes of speciation may also be invoked as an explanation (Wiley, 1981; Wiley and Mayden, 1985).

RESULTS

Cladogram Construction.

A maximum limit was set of 50 equally parsimonious trees to be retained for analysis. The analysis resulted in 50 such trees with length=57. Consensus trees using the strict method (Rohlf, 1982) and the method of Adams (1972) were obtained. The result of the strict consensus tree is depicted in Fig. 2. It has a consensus fork index (Colless, 1980) of $CF=0.704$. The consensus tree of Adams is not shown, because it is very similar to the first one. The only difference is in species *C. lecontei* and *C. melanus* forming a trichotomy with the rest of the *Boreocanthon* species group, instead of being part of it, after having branched from *C. simplex*.

Correlation with Biomes

Maps of the different taxa recognized by Halffter (1958, 1961) and Halffter and Martínez (1977) have been elaborated based on personal collections and publications (Halffter, 1958, 1961; Halffter, and Martínez, 1977; Howden, 1966, Woodruff, 1973). The biomes where the different taxa are distributed generally

have been indicated in the cladogram as well as the probable age of biome appearance (Fig. 2).

TESTS OF ZOOGEOGRAPHIC PREDICTIONS

Taxonomic Congruence

The results of the consensus cladogram have been compared with the accepted classification of the North American groups (Halffter 1958, 1961). These original groups were not based solely on phylogenetic considerations, but represent a classification combining phylogenetic information, morphological distinctiveness and ease of identification. Therefore, it is not surprising that the cladogram does not recover the exact grouping. However, the species sequence of the cladogram agrees in terms of grouping. The cladogram reveals that *Canthon* (*C.*) *obliquus* and *Canthon* (*B.*) *coahuilensis* have a somewhat isolated position regarding the old invasion line of American Canthonina. This situation will be considered in taxonomic terms in a subsequent systematic treatment of the group.

Historical Congruence.

The consensus cladogram (Fig. 2) shows two distinct groups, one composed by the species of the subgenus *Glaphyrocanthon*, which have been used as outgroups for rooting the cladogram and secondly, the ingroup, formed by the subgenus *Canthon* and related taxa, the subgenus *Boreocanthon* and the genus *Melancanthon*. We will start our discussion with the ingroup.

We observe, as expected from our predictions based on the biogeographic hypotheses of the MTZ, that species *C. morsei*, *C. cyanellus*, and *C. indigaceus* branch out at the base of our ingroup and that they are distributed in tropical biomes of Plio-Pleistocene invasion into North America (Fig. 2, Map 1). Their branching order is therefore incongruent with the rest of the ingroup sequence of events if these three species had derived from the same Miocene ancestor that invaded North America from South America and had diversified in biomes that had originated (not invaded) in North America. This lack of congruence supports the assumption that these three species represent separate invaders into North America (Halffter, *op. cit.*). As can be seen from the consensus cladogram (Fig. 2), none of the three taxa are grouped within a clade but form isolated lines in the study area. They represent actually, northern ends of groups whose species richness is centered in South America. *Canthon morsei* (Map 1) is a member of the *juvencus* line (Halffter and Martínez, 1977), all other species of which are South American; *Canthon cyanellus* (Map 1) stems from Colombia, Peru and Venezuela (Halffter, 1961) and its line has a major diversification in South America. These two taxa more probably invaded North America in conjunction with rainforest dispersal into the area and from there *C. cyanellus* expanded its range into other types of tropical forests. *Canthon indigaceus* (Map 2) stems from a diversification process in tropical México (Halffter, 1961). Its three subspecies are limited to tropical conditions, in accordance with the pattern that Halffter (*op. cit.*) has designated typical Neotropical and which is essentially modern in the biogeographic history

of the MTZ. All these species are isolated from the Mexican and North American *Canthonina* (Fig. 2) and are only distantly related to them.

The outgroup, subgenus *Glaphyrocanthon* (Map 3), shows the same type of distribution and biome association as the three above-mentioned invading species. The species *C. (G.) subhyalinus* is distributed from northern Amazonia to southern tropical México and together with *C. (G.) euryscelis*, which is distributed in Central American rainforests, they belong to a line with greatest species diversity in the northern part of Amazonia (Martínez, Halffter and Kohlmann, unpubl.). *Canthon (G.) femoralis* stems from Colombia (Martínez and Halffter, 1972), and *C. viridis* belongs to a species group whose greatest richness is South American (Martínez, Halffter and Halffter, 1964). The northern presence of *Glaphyrocanthon* suggests a concordant expansion with the rainforest, sometimes associated with subspecies formation and penetration into eastern North America (*C. viridis*; Martínez, Halffter and Halffter, 1964). Several other genera of *Canthonina*, such as *Deltochilum*, *Cryptocanthon*, *Pseudocanthon*, *Malagoniella*, and *Megathoposoma* (Halffter and Martínez, 1966, 1967, 1968, 1977; Howden, 1973) follow a pattern of association with tropical biomes, particularly rainforest, reinforcing the Plio-Pleistocene insect invasion hypotheses into the MTZ from South America (Halffter, *op. cit.*).

The consensus cladogram (Fig. 2) shows a recognizable group formed by two main branches, one with *Canthon* species and the other with mostly *Boreocanthon* and *Melanocanthon* species. This group encompasses all those species with an origin stemming from a postulated Miocene invasion into North America. The group conforms also with our prediction that most of the species diversification coincides with the sequence of biome appearances in North America, Miocene events at the root of the group and subsequently a trend toward species association with Pliocene biomes.

The *Canthon* branch includes the "*humectus*" and "*pilularius*" lines of Halffter (1961) and relates them mainly to Miocene events. *Canthon humectus* is distributed in the Mexican Highland in grasslands and arid areas with the exception of the most arid zones, and the highlands of Oaxaca, Chiapas and Guatemala (Map 4). As Halffter (*op. cit.*) indicates, Neotropical species of recent migration have not invaded the highlands; those that do, arrived at the area before its actual rising, a phenomenon that started during the Miocene. The later disruption of their area is attributed by Halffter (*op. cit.*) to the aridity process, which is more recent (Heine, 1973). The *pilularius* line must have colonized the east of the USA during Miocene or somewhat later, but not in recent times. Its actual distribution covers the grasslands of the Great Plains and the forests of the east and south of the country; its distribution nucleus is centered on deciduous hardwood forests (Map 5). Axelrod (1979) indicates that during Middle Oligocene cold winters had eliminated the majority of evergreen dicotyledons in eastern USA, leaving only a deciduous hardwood forest. It was not until the Plio-Pleistocene that prairies and pine forests started to spread (Axelrod, 1979). It is

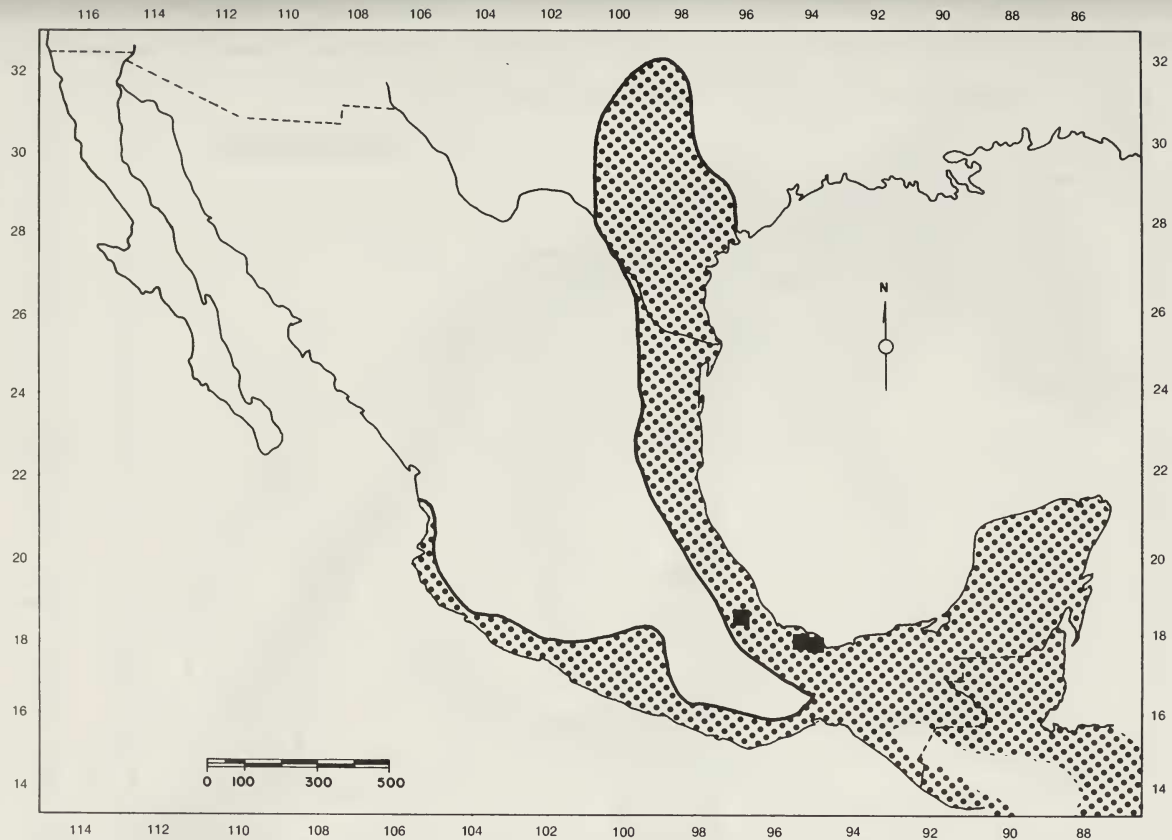
possible therefore, that the *pilularius* line invaded this sort of habitat from the deciduous hardwood forest, explaining the correspondence with the present-day distribution of all four species.

The other branch of the proposed Miocene invasion group includes *Canthon obliquus*, the subgenus *Boreocanthon* and the genus *Melanocanthon*. *Canthon obliquus* is unique (Map 6). It is confined to a relict, deciduous tropical forest (Rzedowski, 1978; Arriaga and Ortega, 1988) at the Sierra de la Laguna in Baja California, having become isolated by the drift process of the Baja California Peninsula. The rift started by late Miocene (Karig and Jensky, 1972) and by early Pliocene separation was very advanced. This species is a relict, since the tropical deciduous forest in which it now lives, was well established in south-central USA during Miocene (Axelrod, 1979) and from that moment it started retreating towards México, its area being steadily reduced. *Canthon obliquus* thence would have become isolated in a remaining island of deciduous tropical forest. Later on, all of the peninsula, with the exception of the southernmost mountains, suffered from desertification and invasions of biota adapted to these conditions, as for *C. (B.) puncticollis*. A similar scheme is known for the *Bursera* (Burseraceae) species from Baja California (Kohlmann and Sánchez-Colón, 1984).

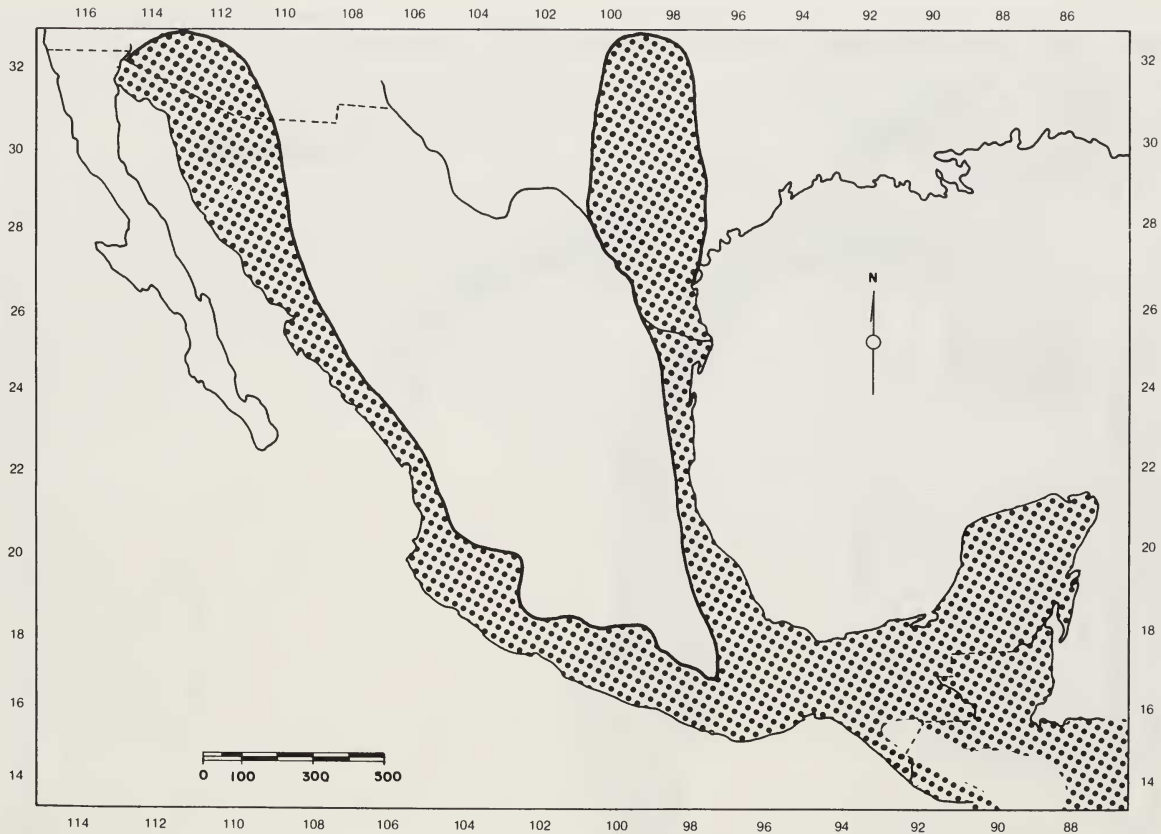
The ancestor of *Melanocanthon-Boreocanthon* would have been distributed originally in northern México and south-central USA, while the area was covered by tropical deciduous forest. By the end of Miocene the forest started to be replaced by grasslands and piñon-oak woodland, a process that was advanced in the Pliocene by the spread of pine forest and very recently the appearance of deserts. Most *Boreocanthon* species (Map 6) live in this area, which leads us to think that this was the main evolutionary arena for this group. Nowadays, many of the species live in grasslands of the Great Plains (*C. simplex*, *C. lecontei*, *C. integricollis*, *C. mixtus*, *C. praticola*, and *C. ebenus*) or in arid zones (*C. puncticollis* and *C. ateuchiceps*). This last species seems to be a recent invader of the arid zones of Puebla, Morelos and Oaxaca following the scheme proposed by Axelrod (1979), where endemic species of the southern arid zones of México are recent relicts, which have been pushed into these areas by climatic events of the late Cenozoic (Heine, 1973). One species, *C. melanus*, apparently is confined largely to the Arizona mountains in piñon-oak woodland, although there is one record from Guaymas, Sonora, for the coastal desert. Two species, *C. probus* and *C. depressipennis*, follow a similar pattern to *Melanocanthon*; in addition to being present in the Great Plains, both penetrate into eastern USA through the conifer forest corridor. This distribution could represent an invasion from the grasslands into the conifer forest corridor. With the exception of these two species, all the rest of *Boreocanthon* is associated with biomes that originated in the Miocene.

The last group, *Melanocanthon* (Map 7) is associated mostly with Pliocene biomes. The only species associated exclusively with a Miocene biome is *M. nigricornis*, which is distributed in the grasslands of the Great Plains. The remainder occur in the conifer forest corridor in the south and east of the USA (*M.*

bispinatus); in the grasslands and conifer forests of Texas and northern Florida (*M. granulifer*); or else in northern Florida (*M. punctaticollis*). The invasion and speciation process seems to have shifted to the east in this group, relative to the other south-central diversification areas and follows the pine and pine-oak forest corridors that established themselves around the deciduous forests. It seems to be the only member of the Miocene group whose speciation events are recent (Pliocene), whereas in *Canthon* and *Boreocanthon* some species seem to have invaded but not speciated in Pliocene biomes. The invasion and speciation pattern in *Melanocanthon* is somewhat similar to that of *Ateuchus* (Coleoptera: Scarabaeidae), since it is proposed that the latter genus invaded and diversified in an approximately similar zone in Plio-Pleistocene time (Kohlmann and Halffter, 1988).



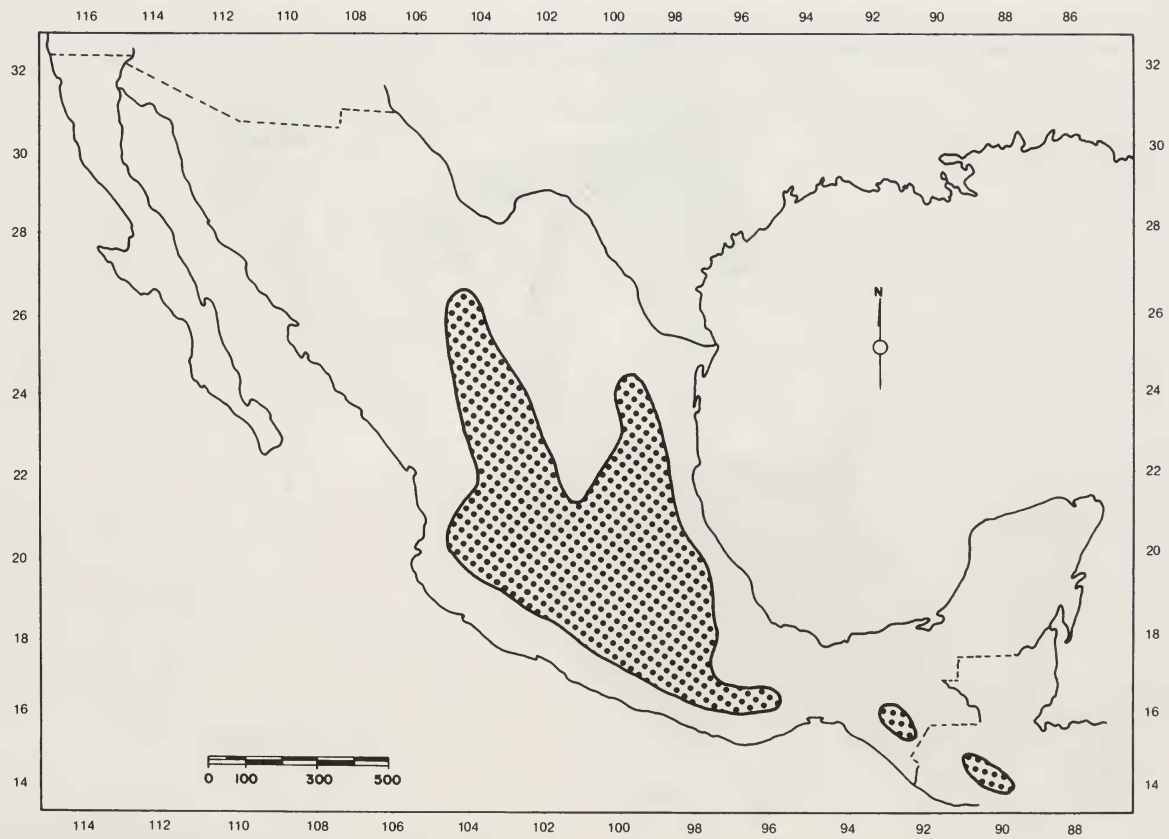
Map 1. Geographical distribution of the *C. (Canthon) cyanellus* line in northern Middle America and in southern United States of America. Black squares represent the known localities for *Canthon morsei*.



Map 2. Geographical distribution of the *C. (Canthon) indigaceus* line, in northern Middle America and in southern United States of America.



Map 3. Geographical distribution of *C. (Glaphyrocanton)* in northern Middle America and in southern United States of America.

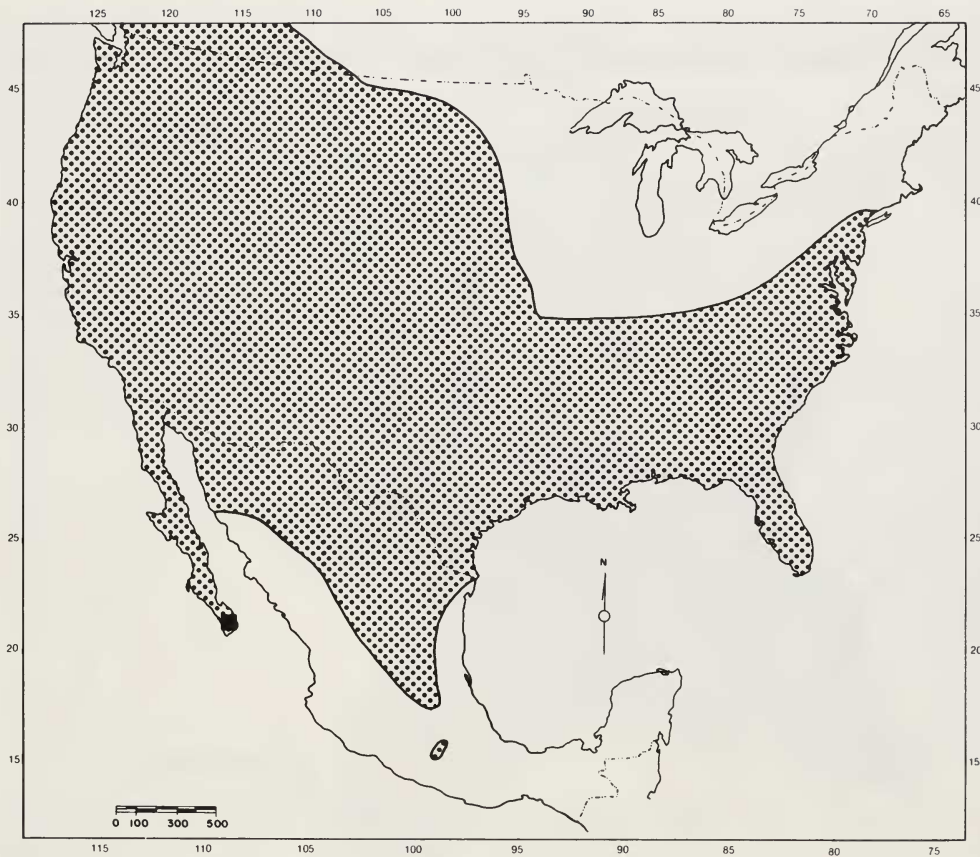


MAP 4. Geographical distribution of the *C. (Canthon) humectus* line in Mexico and Guatemala.

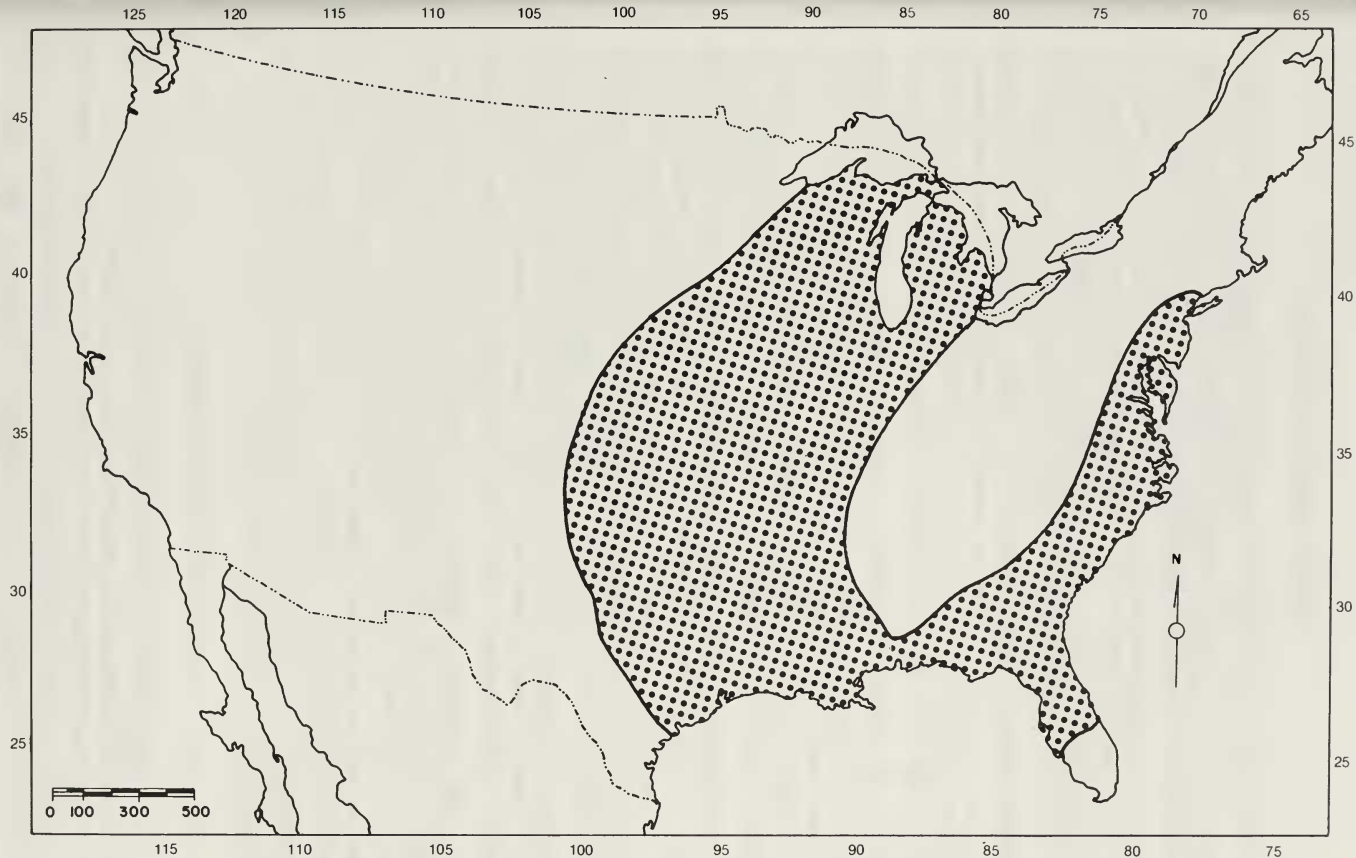


Map 5. Geographical distribution of the *C. (Canthon) pilularius* line in Mexico and in the United States of America.

Map 4. Geographical distribution of the *C. (Canthon) hololepis* line in Mexico and Eastern



Map 6. Geographical distribution of *C. (Boreocanthon)* in Mexico and in the United States of America. The square at the bottom end of the peninsula of Baja California represents the distribution of *C. (Canthon) obliquus*.



Map 7. Geographical distribution of *Melanocanthon* in eastern United States of America.

CONCLUDING STATEMENT

We observe from the previous analysis that the concordance of the consensus cladogram with the age of appearance of the different biomes is congruent with our predictions based on the biogeographical hypotheses of the MTZ. Therefore this fact may be considered supportive of the supposition of two different insect invasion waves from South into North America. Moreover, the analysis points to a strong correlation between a great diversification of the Miocene invasion lineage with biomes that started to originate in the Miocene. Far fewer species are associated with Pliocene biomes, and in several of such seem to represent secondary invasions. Finally, no species stemming from the proposed Miocene invasion have been found in Pleistocene biomes (tropical rainforest). This would suggest that ball-rollers of the Miocene invasion have not had enough time to diversify in this new environment, or that most probably ecological replacement stemming from the many South-American-derived species living in tropical forests in North America have precluded species diversification effectively.

This analysis may be corroborated by other studies. However, not many insect examples with a suspected similar history are known. The scarabaeid genus *Phanaeus* seems to follow a related pattern (Halffter, 1962; Edmonds, 1972). This genus is being revised by Edmonds (pers. coms.), and a similar analysis may be very illuminating. Savage (1982) already has presented evidence for a late Cretaceous and a Plio-Pleistocene dispersal of South American fishes, amphibians and reptiles into Central America. For floras, Gentry (1982) also proposes two migrations of Neotropical floristic elements from South to North America. Gentry (1982) considers that the two main waves occurred at the end of the Cretaceous and then again in Pliocene. The history of the dung-rollers seems to be more similar to the one postulated for mammals (Stehli and Webb, 1985), where an increasing frequency of connection started in Miocene and culminated in Plio-Pleistocene. At any rate the existence of two different invasion processes is supported by the present analysis for the dung-rollers, although the exact timing of the first wave may be debatable still. In conclusion we would consider that the approach presented here may be of help in other situations where several invasion or dispersal waves in different taxa are suspected.

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APPENDIX

The phenetic analysis of the American canthonine genera and subgenera of *Canthon* (Fig. 1) is based on the work of Halffter and Martínez (1966, 1967, 1968 and 1977). Seventy-one characters of external and internal structures have been taken into consideration; thirty-two of them are binary and thirty-nine are multistate. The distribution of these characters and their description are available from the authors.

Some problems exist in the analysis. The male of *Canthotrypes* is not known. The aedeagus of *Zonocopriss* and *Deltepilissus* could not be examined.

The phenogram (Fig. 1) was elaborated using the UPGMA method. As a distance measure the Manhattan coefficient was used. This coefficient implies the existence of orthogonal axes. The character correlation matrix (not reproduced) has low correlation values, therefore this metric is acceptable.

The analysis of the phenogram indicates various groups:

Tetraechma-Xenocanthon-Pseudepilissus-Canthonidia; *Vulcanocanthon-Holocanthon*; *Melanocanthon-Boreocanthon -Nesocanthon-Canthon*; *Anisocanthon-Trichocanthon-Scybalocanthon*; *Deltepilissus-Francmonrosia-Goniocanthon*; *Hansreia-Peltecanthon-Scybalophagus*; *Zonocopriss-Pseudocanthon*; *Sylvicanthon-Glaphyrocantthon*; *Sinapisoma-Paracanthon-Canthonotrypes-Agamopus*; *Megathopa-Megathoposoma*; and the following isolated lines - *Canthochilum*, *Canthonella*, *Cryptocanthon*, *Deltochilum*, *Eudinopus* and the most removed one, *Streblopus*. It should be mentioned here that *Deltochilum* is a very heterogeneous entity.

The ladder structure in the phenogram suggests that the relationships between taxa is a very gradual one, implying that the group is very homogeneous in its morphological characteristics. The low morphological character correlation seems to indicate that there has not been any tendency to form groups of associated characters.

Until a detailed cladistic analysis is performed, the present study should be considered as preliminary.

TABLE 1

Morphological Characters Used in the Study of North American *Canthonina*

- 1.- Number of elytral striae. Usually eight: a; usually nine: b.
- 2.- First article of the metatarsi. Usually bigger than the second: a; usually shorter than the second: b; equal: c.
- 3.- Anterior margin of the metafemur. Without margin: a; with margin: b.
- 4.- Elytra. Translucent: a; opaque: b.
- 5.- Clypeo-genal suture. With broad external notch: a; with narrow external notch: b.
- 6.- Subhumeral stria. Usually not keeled: a; usually keeled: b; usually slightly keeled: c.
- 7.- Number of clypeal teeth. No teeth: a; bidentate: b; quadridentate: c.
- 8.- Clypeal teeth separation. Narrowly separated: a; widely separated: b.
- 9.- Separation between proepisternum and proepimeron. Without a keel: a; keeled: b; slightly keeled: c.
- 10.-Proepisternum. Shallowly excavated: a; excavated: b.
- 11.-Prescutellar impression. Usually not marked: a; usually marked: b.
- 12.-Dorsal surface. Usually not granulated: a; usually granulated: b.
- 13.-Granules. Simple: a; like shining spots: b; flattened: c; elongated: d.
- 14.-Pronotum. Without punctuation: a; with punctuation: b.
- 15.-Protibia straightly truncate: a; obliquely truncate: b.
- 16.-Eyes. Narrow: a; wide: b.
- 17.-Metatibia. With one spine: a; with two spines: b.
- 18.-Separation between gula and submentum. Narrow "V": a; wide "V": b; arched: c.
- 19.-Elytral external striae. As deep as the internal ones: a; deeper than the internal ones: b.
- 20.-Dorsal eye margin. With border: a; without a border: b.
- 21.-Dorsal eye margin. Bordered by a wide flat band: a; bordered by a raised fold: b.
- 22.-Ventral clypeal structure. With a tooth: a; without a tooth: b.
- 23.-Protibia. Not widened along its internal margin: a; widened along its internal margin: b.
- 24.-Mesosternum. Short: a; very wide: b.
- 25.-External margin of the clypeo-genal suture. Straight or slightly pointed: a; with an evident tooth: b.
- 26.-Lateral pronotal margin. Usually not serrated: a; usually serrated: b.
- 27.-Posterior angle. Pointed: a; blunt: b.
- 28.-Elytral margins. Slightly curved upwards behind the humeral angle: a; strongly curved upwards behind the humeral angle: b.
- 29.-Elytral colour. Orange: a; not orange: b.

?= Character not applicable.

TABLE 2

Character distribution in the North American *Canthonina* species

Melanocanthon punctaticollis (Schaeffer)	BAABAACBAAABBBAAABAAABABAAABAB
Melanocanthon nigricornis (Say)	BAABAACBAAABCBAABAAABABAAABAB
Melanocanthon granulifer (Schmidt)	BAABAACBAAABABAAABAAABABAAABAB
Melanocanthon bispinatus (Robinson)	BAABAACBAAABDBAABAAABABAAABAB
C. (Boreocanthon) simplex LeConte	BAABAACBAAABBBAAAAAABBBBABABAB
C. (Boreocanthon) ateuicheps Bates	BAABBBCBAAAA?BAAAAAABBBABABAB
C. (Boreocanthon) depressipennis LeConte	BAABBACBAAABAAAAAABBBABBBAB
C. (Boreocanthon) ebenus (Say)	BAABBACBAAABAAAAAABBBABBBAB
C. (Boreocanthon) praticola LeConte	BAABBBCBAAABAAAAAABBBABBBAB
C. (Boreocanthon) integricolis Schaeffer	BAABBBCBAAABBBAAAAAABBBABABAB
C. (Boreocanthon) mixtus Robinson	BAABBBCBAAABBBAAAAAABBBABABBB
C. (Boreocanthon) lecontei Harold	BAABABCBAABBAAAAAAABBBBABABAB
C. (Boreocanthon) melanus Robinson	BAABABCBAABBBAAAAAABBBBABABAB
C. (Boreocanthon) probus Germar	BAABBBCCBAAABBBAAAAAABBBBABABAB
C. (Boreocanthon) puncticolis LeConte	BAABBBCBAAABBBAAAAAABBBBABABAB
C. (Boreocanthon) coahuilensis Howden	BAABAACBAAAA?BAAAAAABBBAAABAB
C. (Canthon) obliquus Horn	BABBAAA?AABA?BAAAAAABBAABAB
C. (Canthon) chalcites (Haldeman)	BABBAAABBAABAAAAABAAABBAABAB
C. (Canthon) vigilans LeConte	BABBAAABBAABAAABABAAABBAABAB
C. (Canthon) imitator Brown	BABBAAABAAAAABAAAAABBAABAB
C. (Canthon) pilularius (Linnaeus)	BABBAAABBAABAAAAABAAABBAABAB
C. (Canthon) humectus (Say)	BABBAAABBBBABAAACAABBAABAB
C. (Canthon) indigaceus Harold	BABBAAABAAAA?BAAACAABBAABAB
C. (Canthon) cyanellus LeConte	BABBABCACABA?BBAACAABBAABAB
C. (Canthon) morsei Howden	BBBBAABACAAA?BBAACAABBAABAB
C. (Glaphyrocantion) subhyalinus Harold	BBAAAABABBAA?BBAACAABAAAAAAB
C. (Glaphyrocantion) euryscelis Bates	BBAAAABABBAA?BBAACAABAAAAAAB
C. (Glaphyrocantion) viridis (de Beauvois)	BBABAABABBAA?BAAACAABAAAAAAB
C. (Glaphyrocantion) femoralis (Chevrolat)	ABABAACABBAA?AAAAACAABAAAAAAB

